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Phytoplankton in a turbulent world*

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SUMMARY: This contribution reviews relationships between turbulence and marine phytoplankton ecology, ranging from the mesoscale to the smallest scales. Phytoplankton life-forms, considered to be survival strategies in a turbulent environment, are briefly presented. The importance of mesoscale hydrodynamics on phytoplankton distributions and organisms physiology and behaviour, are examined. Finally, direct effects of small scale turbulence on phytoplankton are considered.

Key words: Phytoplankton, life-forms, turbulence, dinoflagellates.

INTRODUCTION

Photosynthetic production of organic matter is fueled by solar energy. However, primary production can only be sustained if the necessary factors (such as organisms, light and nutrients) are brought together. In the aquatic environment, this role is fulfilled by water motion, largely driven by solar energy, through heat or momentum transfer by the wind. The auxiliary energy provided by mechanical water movement has been called external energy, in contrast with the internal energy involved in cell metabolism (Margalef, 1978).

Water motion occurs in the marine environment at all spatio-temporal scales (Denman and Gargett, 1983). The cascade of physical variability in the ocean begins with processes such as the creation of eddies by instabilities of the mean gyre circulation. The introduced turbulent kinetic energy is transmitted from large to progressively smaller scales, down to the viscous domain and the associated conversion of turbulent kinetic energy into heat (Woods, 1980).

The planktonic way of life implies, by definition, suspension and drifting in water. Thus, the hydrodynamic properties of the aquatic environment play a fundamental role in plankton ecology. The modes of interaction between water motion and phytoplankton organisms are diverse. At large scales relative to the size of the organisms, water motion controls the transport both of the organisms themselves and of relevant physico-chemical properties of the water. Examples can be found at a wide range of spatial dimensions. The coastal regions at the western margin of the continents are highly productive zones due to upwelling of nutrient-rich water caused by wind forcing and basin-wide patterns of current circulation. Mesoscale features like jets, gyres and fronts provide mechanisms for nutrient injection and enhanced production in the upper layers (Horne and Platt, 1984; LeFèvre and Frontier, 1988). At small scales relative to the organisms, turbulent water

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movements affect the transport of molecules in and out of the cells and may have direct effects on processes such as cell division or grazing by herbivorous organisms.

The aim of this contribution is to review some aspects of the relationships between water turbulence and phytoplankton ecology. The emphasis will be on marine phytoplankton, although most concepts can be equally applied to the phytoplankton of continental waters. We shall present first a description of the main phytoplankton life-forms, considered as adaptations to a combination of environmental factors in which turbulence plays a basic role. The second section will be devoted to the coupling between mesoscale hydrodynamics and variability in the horizontal and vertical distribution of phytoplankton. Next, we will comment on the interactions of turbulence with factors such as light penetration and supply of nutrients, and their consequences for organism behaviour and physiology. Finally, the last section will address some direct effects of small scale turbulence on phytoplankton cells. Aspects concerning interactions with other components of the planktonic food web have been discussed in other chapters of this volume.

PHYTOPLANKTON LIFE-FORMS AND EXTERNAL ENERGY

The functional significance of the rich morphological diversity of phytoplankton has attracted much attention from planktologists. Critical reviews of the subject can be found in Sournia (1982), Elbrächter (1984) and Fogg (1991). A classical approach (Schütt, 1892; Gran, 1912) recognized morphodynamic categories such as bladder, ribbon, hair, branching and mucous. These shape types may be applied to cells or colonies of many size classes and represent only one of many possible classifications of the variety of morphological features found in phytoplankton. Properties like shape, surface/volume ratios or possession of appendages have been variously interpreted as adaptations to prevent sinking, to increase nutrient assimilation or to avoid grazing. The implications of size in relationship to sinking rates have been thoroughly discussed (Smayda, 1970; Kiørboe, 1993), but the implications of the physiological properties of the organisms are much less obvious (Banse, 1982; Tang 1995). It appears that many morphological and functional features of phytoplankton are relevant to environmental turbulence (Margalef, 1978, 1997; Fogg, 1991). However, as pointed out by Sournia (1982) and Elbrächter (1984) among others, conceptual and experimental work regarding the significance of such categories is lacking.

A general approach to the systematization of phytoplankton life-forms has been proposed by Margalef (1978), who defined them as "the expression of adaptation syndromes of organisms to certain recurrent patterns of selective factors". Taking into account the overwhelming importance of external energy, Margalef (1978) proposed a systematization of the functional morphology of phytoplankton on the basis of two basic environmental factors: supply of nutrients and intensity of turbulence. This conceptual model has been expressed in graphic form by Margalef in a so-called phytoplankton mandala (Margalef, 1978; Margalef *et al.*, 1979), and has provided a robust framework for ecological interpretation (Fig. 1). Major taxonomic groups of phytoplankton occupy different spaces within the mandala. Diatoms, non-motile and with fast potential growth rates thrive in relatively turbulent, nutrient-rich waters. Under these conditions, lack of motility is compensated by resuspension of cells due to turbulence and high growth rates. Dinoflagellates, which are motile due to the possession of flagella, can regulate their position in the water column. This allows for survival in stratified waters, where motility and migration behaviour may override sedimentation and contribute to the acquisition of nutrients from deep layers. Other phytoplankton groups, such

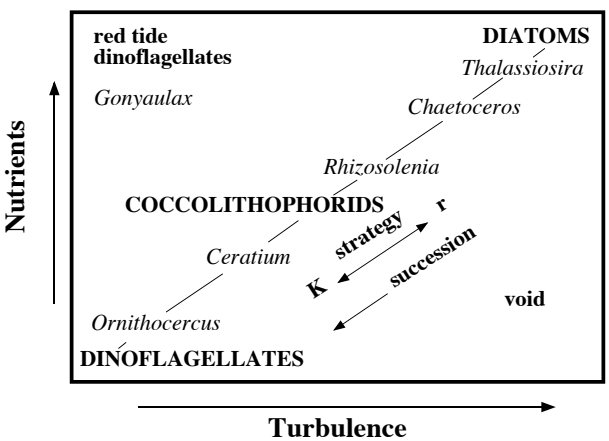

FIG. 1. – Margalef's Mandala. Graphic representation of the main phytoplankton life forms in an ecological space defined by nutrient concentration and turbulence. Redrawn from Margalef (1978).

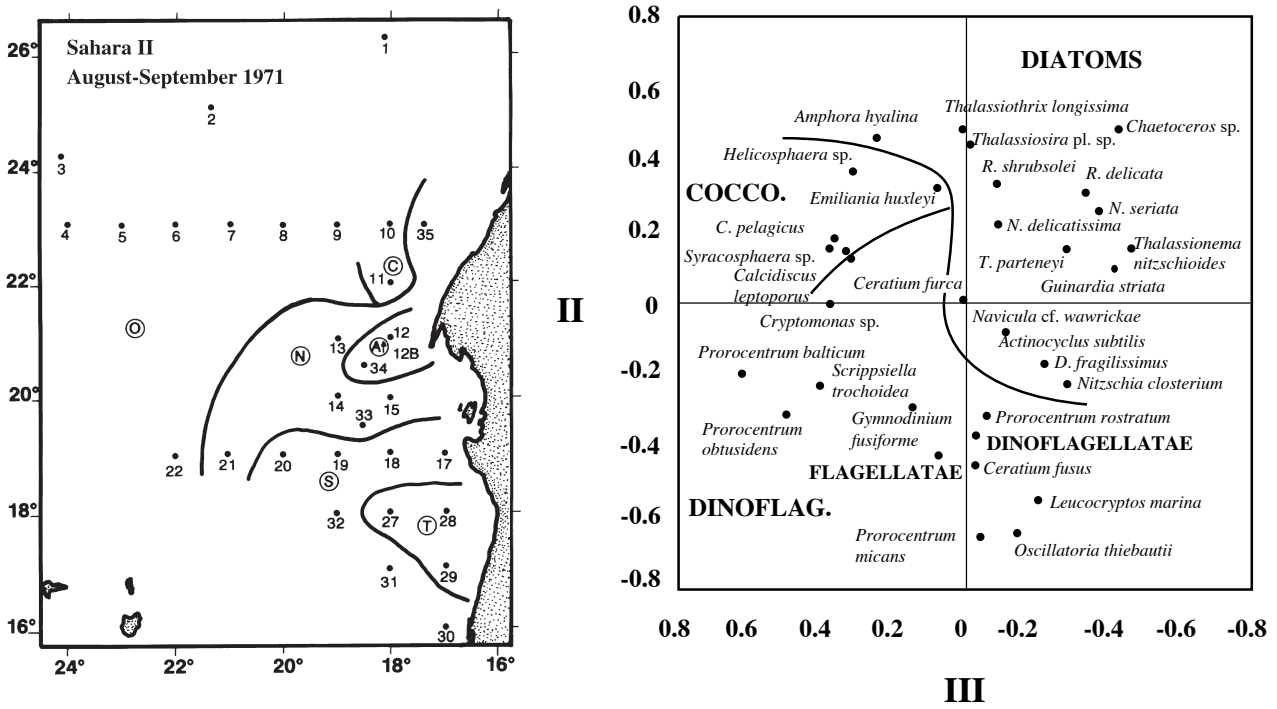

FIG. 2. – Left: Area of study in NW Africa covered by the *Sahara II* cruise in 1971. Numbers indicate the location of the sampling stations . Letters refer to hydrographically defined water masses. Right: Plot of species and groups of species according to their correlation coefficients with the second (II) and third (III) component axes of a Principal Component Analysis. Redrawn from Margalef and Estrada (1981).

as the coccolithophorids appear to occupy intermediate positions. For each major life-form, differences in size would represent an expansion of the basic niche space. In terms of Margalef's mandala, a typical phytoplankton succession (Margalef, 1978) would follow a trend from the high turbulence-high nutrient corner to the opposite low-turbulence-low nutrient corner. Red tides tend to appear in the rather anomalous situation of high nutrients-low turbulence, which favours motile forms.

The relationships between the distribution of phytoplankton assemblages and environmental conditions can be evidenced by using multivariate statistical techniques based on species abundance distributions. For example, a Principal Component Analysis performed on phytoplankton samples taken from the upwelling region of NW Africa (Margalef and Estrada, 1981) showed a striking association of the species into taxonomic groups, reflecting a similar ecological response (Fig. 2). In turn, these groups (i.e. diatoms, coccolithophorids and dinoflagellates) were clustered on the plane defined by components II and III, a statistical space that corresponds to the basic inshore to offshore gradient of external energy in the upwelling environment. It can be observed that the distribution of the organisms agrees with the conceptual model of Fig. 1. Similar results have been found in studies on phytoplankton assemblages in other areas (Estrada, 1991) or even in microcosm experiments (Estrada *et al*., 1988). Other examples of relationships between community changes and hydrographical conditions of the environment can be found in Reynolds (1984) and Harris (1986). Overall, the mentioned studies illustrate that phytoplankton organisms can also be seen as sensors of the environment, with the advantage of being able to provide integrated responses at scales commensurate with their life-times.

One of the difficulties for the application of conceptual models like Margalef's mandala to real data is the quantification of the variables involved. One of the few attempts made in this direction is the interpretation by Bowman *et al*. (1981) of the phytoplankton distributions in Long Island Sound. In their study, the potential growth rates of the organisms were represented in a diagram defined by optical depth ($k \cdot h$, the product of the light attenuation coefficient, k by depth, h) and turbulence intensity, as expressed by the stratification index proposed by Simpson and Hunter (1974). A similar method was used by Jones and Gowen (1990) for data from coastal areas of the British Isles. Another approach to cast real data on Margalef's mandala has been proposed by M.A. Rodríguez (pers. comm.). The

potential production axis was expressed as the covariance between irradiance and biomass profiles (see Margalef, 1997) and the nutrient concentration axis was represented by a quotient between the product of normalized concentrations of nitrate and silicate (phosphate was not considered due to lack of data) and a stability index.

MESOSCALE OCEANIC TURBULENCE AND PHYTOPLANKTON ECOPHYSIOLOGY

This section will emphasize the significance of intermediate scale (from a few metres to several kilometres) turbulence on phytoplankton physiology and distribution. Water motion may entrain phytoplankton cells but often their observed distributions are not a passive result of water movements. Vertical mixing, in particular, has a direct relevance to phytoplankton physiology because it determines light penetration and supply of nutrients. By affecting the primary producers, water motion affects the organization of the whole planktonic ecosystem in the oceans.

Mesoscale (of the order of 10-100 km) variability in the oceans is based on features such as gyres, upwellings and fronts. Sources for microscale (a few centimetres) and finescale (a few metres) turbulent motion near the surface and in the stratified part of the ocean include breaking of both surface and internal gravity waves, free and wind forced convection, thermohaline intrusions (which result in high dissipation of kinetic energy at the boundaries) and salt fingering (Yamazaki and Osborn, 1988; Owen, 1989). More detailed accounts of the ecological role of these environmental features can be found in texts by Harris (1986) or Mann and Lazier (1991).

Horizontal patchiness

Plankton distributions in the oceans are highly heterogeneous. This patchiness is generated by the interaction between hydrographical variability, which may entrain active or passive particles suspended in the medium, and the biological response of the organisms, which cannot be considered as passive tracers. In general, the meso- and small scale distribution of the organisms reflects the physical variability of the environment derived from the mechanisms mentioned above; however, biological responses due to growth, motility and interaction between organisms, which are typically non-linear, become superimposed on the perturbations originated by the physico-chemical fluctuations of the environment (Estrada, 1978). The response of phytoplankton organisms to physical perturbations is basically mediated by modifications in the supply of light and nutrients, which originate pulses of growth (see next section). As a result, phytoplankton distributions tend to appear as peaks of high abundance on a low population density background (Margalef, 1976).

Phytoplankton patchiness is relevant for the whole planktonic ecosystem (Davis *et al.*, 1991). For example, due to threshold phenomena in their feeding mechanisms, planktivores may be more able to survive with a patchy distribution of prey than with an homogeneous distribution on the same average population density (Owen, 1989). In addition, microscale turbulence may directly affect food web interactions, as described in detail in this volume by Kiørboe and by Alcaraz.

In recent decades, the incorporation of automated methods allowing continuous measurement of fluorescence and other parameters, as well as the utilization of remote sensing methods have provided a wealth of information concerning the horizontal distribution of phytoplankton over a wide range of scales. One of the most influential studies in this field was published by Platt (1972), who found that the power spectrum of fluorescence fluctuations followed the -5/3 slope predicted by Kolmogorov (1941) for fully developed turbulence in the inertial subrange. Later studies applied time series methods to phytoplankton of lakes (Powell *et al.*, 1975) and estuaries (Lekan and Wilson, 1978), as well as to distributions of physico-chemical variables and organisms of higher trophic levels (Denman, 1976; Estrada and Wagensberg, 1977; Mackas and Boyd, 1985). Gower *et al.* (1980) used LANDSAT multispectral scanner imagery to estimate phytoplankton abundances and used them as indicator of mesoscale water motions. They found that the fluctuation spectra followed approximately a $k^{-2.92}$ law and concluded that this result was consistent with the behaviour of phytoplankton as a passive scalar of ocean currents. This affirmation was challenged by Lesieur and Sadourny (1981), who showed that a passive scalar should follow the well known $k^{-5/3}$ power law; they conceded, however, that the presence of intermittence could yield a steeper slope.

Vertical structure of the water column and phytoplankton distribution

The vertical structure of the water column involves a delicate balance between destabilizing forces (derived from wind stress and heat loss at the surface and shear at the base of the mixed layer) and stabilizing effects (such as surface buoyancy gain due to heating or freshwater influx) (Denman and Gargett, 1995). The typical vertical profile of the upper ocean, with a surface mixed layer on top of a layer of sharp density gradient or pycnocline, is associated with large variations in the intensity of turbulent energy dissipation and has important effects in controlling nutrient supply and vertical phytoplankton distribution (see below). A typical feature, in stratified waters, is the presence of a deep chlorophyll maximum (DCM) located within the pycnocline, where vertical dispersion of the organisms is reduced (Cullen, 1982; Estrada, 1985a). In oligotrophic areas like the Mediterranean Sea, the DCM is associated with a sharp gradient of increasing (in the downwards direction) nutrient concentration and is located at depths receiving approximately 1% of surface irradiance. Phytoplankton growth rates at this level are relatively low (Estrada, 1985b), but breaking of internal waves or other instabilities, which throw nutrient-rich waters to upper levels, may allow for pulses of enhanced growth which originate a patchy distribution at the DCM level (Goldman, 1988; Berdalet and Estrada, 1993). Other types of subsurface chlorophyll maxima may be due to active swimming and depth regulation by the organisms, in relationship to the vertical distribution of nutrients, light, density, turbulence or other factors (layer-formers of Cullen and MacIntyre, in press).

Modelling approaches

The usual way of simulating the interaction between hydrographical processes and plankton organisms requires the combination of the Navier-Stokes equations of water motion, or simplified versions of them, with expressions describing the growth and interactions among the relevant biological species or categories (Riley *et al*., 1949; Denman and Platt, 1976; Powell and Okubo, 1994).

A simple model for the case of a population exposed to losses by diffusion or dispersion (the so-called KISS model) was proposed by Skellam (1951) and Kierstead and Slobodkin (1953). The formulation of Kierstead and Slobodkin (1953) establishes a relationship between growth rate of phytoplankton in a favorable patch and dispersion processes tending to erode biomass accumulation. For certain boundary conditions, this model predicts a characteristic length scale (the KISS length) for the minimum size of the patch needed to maintain the population. The KISS model has some unlikely assumptions, such as that turbulence is isotropic at scales larger than a few metres and that growth rates are uniform throughout (Mackas *et al*., 1985). However, it has provided a useful conceptual framework for processes such as red tide formation (Wyatt and Horwood, 1973).

Systems of differential equations combining reaction (biological growth and interactions) and diffusion terms may contain non-linearities which originate *symmetry-breaking instabilities* or *dissipative structures* (Levin and Segel, 1976; Dubois, 1975; Okubo, 1980) when perturbations exceed a certain critical size (which is homologous to the critical length of the KISS model). However, it is doubtful whether such instabilities inherent to the system play a relevant role in the natural aquatic environment, which is strongly subjected to external forcing (Estrada, 1976).

Attempts to use mathematical reasoning to deduce regularities concerning the coupling between physical variability and biological response have been made among others by Denman (1983) and Powell and Okubo (1994). The question is not simple. In the case of one species in a turbulent environment, the general result is that patchiness at small scales ($k >> k_c$, where k is the wavenumber, i.e. the inverse of the Kolmogorov length scale and k_c is the wavenumber corresponding to the KISS length) has the same shape as environmental turbulence; i. e., is totally controlled by physics. At large scales, the power spectrum of plankton abundance presents less patchiness intensity; i. e. is "flatter" than that of environmental turbulence fluctuations (Denman *et al*., 1977; Powell and Okubo, 1994). At $k=k_c$ there is a singularity indicating high patchiness at length scales close to the KISS length. However, in the case of interacting species, the power spectrum of concentration fluctuations may be flatter or steeper than the physical spectrum, depending on the characteristics of the diffusion field (Powell and Okubo, 1994). Thus, the establishment of broad generalizations on the basis of observed power spectra does not appear to be feasible.

Vertical mixing and primary production

Vertical mixing favors phytoplankton growth by injecting nutrients from deeper layers into the euphotic zone. However, if turbulence becomes too intense, the phytoplankton cells are entrained to dark zones of the water column and may not receive enough light to carry out their photosynthetic activity. A key concept is that of *critical depth* (Gran and Braarud, 1935; Riley, 1942; Sverdrup, 1953) which represents the depth at which the sum of gross photosynthesis between this depth and the surface equals phytoplankton respiration. This critical depth (Z_c) has to be compared with the depth of the mixed layer (H). In principle, phytoplankton biomass will only increase if $Z_c > H$. An expression of these relationships is the seasonal cycle of temperate regions, which typically presents an autumn peak, when the summer thermocline starts to break down, and a winter spring peak, when the thermocline starts to form. In these situations, nutrient inputs coincide with sufficient stability for phytoplankton growth. An example of these relationships in space, are the upwelling regions, which present an inshore to offshore gradient of decreasing turbulent mixing. In a transect perpendicular to the NW Africa upwelling (Fig. 3), the maximum phytoplankton biomass (in terms of chlorophyll concentration and cell numbers) occurred at the mid shelf, at intermediate values of turbulence (Estrada and Blasco, 1985). In comparison, lower phytoplankton biomasses were observed close to the coast, where strong mixing and high water turbidity hindered phytoplankton growth, and offshore, where thermal stratification decreased nutrient supply. Gradients of dissipation of physical energy at levels compatible with biological responses can be found at many space and time scales. These features have been called ergoclines by Legendre and Demers (1985).

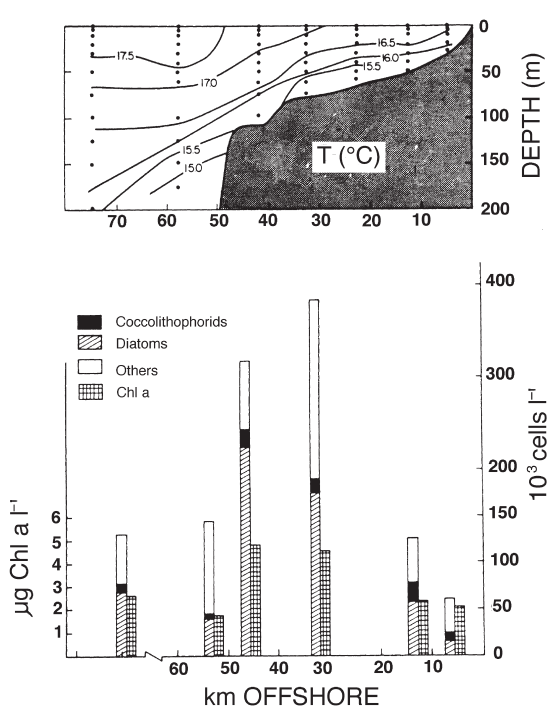

FIG. 3. – Above: Mean temperature distribution for the R/V Atlantis cruise 82 (March-May 1974) along the 21° 40' N line across the NW Africa upwelling. Below: Average numbers for the upper 10 m of coccolithophorids, diatoms, cells of all other groups, and chlorophyll concentrations at the 21° 40' N line. Redrawn from Estrada and Blasco (1985).

Vertical mixing and photoacclimation

The entrainment of phytoplankton by water motion exposes the organisms to continuously varying irradiances. This environmental forcing interacts with the ability of organisms to change their photobiological properties. This phenomenon, known globally as photoacclimation (Kirk, 1994), is complex and consists of processes occurring at several time scales. It is easy to understand that if the time scale of displacements due to water turbulence is shorter than that of the fastest photoacclimation mechanisms, algae at all depths within the mixed layer would exhibit similar properties. On the contrary, in completely stagnant water, algae at every depth would show different behaviour. The situation in nature is intermediate, leading to expect a relationship between the variability of different indices of photoacclimation with depth and the intensity of turbulent mixing. A conceptual model of this relationship was proposed by Lewis *et al*. (1984a) who defined two non-dimensional numbers to express the ratio of the mixing rate to the photoacclimation rate. Direct measurement of photacclimation properties of phytoplankton at different levels of turbulent kinetic energy dissipation (Lewis *et al*., 1984b) showed that this parameter was a strong determinant of algal photosynthesis in the upper mixing layer. More available information on the relationship between photosynthesis and turbulence can be found in Kiørboe (1993).

Sinking, swimming and suspension

The physical structure of the water column has relevant implications for the suspension of plank-

tonic organisms. Swimming speed of motile phytoplankton is of the order of 12-20 m d^{-1}, while sinking velocity is of the order of 1 m d^{-1} for actively growing cells (Sournia, 1982; Bauerfeind *et al.*, 1986). Thus, motile cells would remain suspended in the water column in a completely laminar system, whereas, as discussed below, they would be entrained by water movements at typical turbulence levels in the sea (Reynolds, 1994).

A simple model of particle deposition (Smith, 1982) is based on the idea that the water column is completely mixed at intervals, while particles (or non-motile organisms) settle between mixings. In fully developed turbulence, particles entrained in a mixed layer of thickness h_m become progressively diluted, according to the expression (Smith, 1982; Reynolds, 1994):

$$n_t/n_0 = exp(-w_s t/h_m)$$

where w_s is the sinking velocity and n_0 and n_t are the number of particles at times *0* and *t*, respectively. Thus, non-motile cells must compensate with growth rates exceeding the rates of sinking loss (Reynolds, 1994). A more sophisticated approach to the problem of suspension in a turbulent environment was presented by Lande and Wood (1987), who used diffusion theory to derive general formulae for the expected time that a particle would spend in the mixed layer. They allowed for resuspension of particles from the top of the thermocline and found that the total time spent in the mixed layer was greatly increased for particles which reduced their sinking rate in the thermocline.

The behaviour of non-motile phytoplankton in natural conditions is much more complex than simple deposition theories may lead to expect. There are interactions between sinking speed and physiology. For instance, actively growing cells sediment more slowly that dead cells (Steele and Yentsch, 1960; Bienfang *et al.*, 1983). In addition, non-motile phytoplankton forms may have means of buoyancy regulation, for example through possession of gas vacuoles (Oliver 1994), changes in their chemical composition (Villareal, 1988) and physiology (Anderson and Sweeney, 1977; Waite *et al.*, 1992). In the case of actively moving flagellates, the intensity of turbulence will compete with their swimming abilities. The degree of entrainment has been examined by Reynolds (1994), who concluded that turbulence in mixed layers was usually adequate to disperse algae, while buoyancy regulation and swimming could play a dominant role in stratified waters. Aspects of motile phytoplankton behaviour in relationship with water motion have recently been reviewed by Kamykowski (1995) and Kamykowski *et al.* (in press). Cullen and MacIntyre (in press) identified three general phytoplankton strategies (mixers, migrators and layer-formers) concerning physiology and depth regulation and discussed their relevance in the context of harmful algal blooms.

EFFECTS OF SMALL SCALE TURBULENCE

This section will give a brief account of aspects relating small-scale turbulence to nutrient uptake by phytoplankton, formation of microzones in a fluid environment and direct effects on cell growth. Other relevant questions, such as the role of turbulence on formation of plankton aggregates (Jackson, 1994; Kiørboe *et al.*, 1990) and predator-prey relationships (e.g. Alcaraz, 1997; Kiørboe, 1997; Sundby, 1997) will not be discussed here.

As preliminary information, it should be emphasized that phytoplankton cells are typically smaller than the Kolmogorov length in aquatic environments, so that the velocity field in their vicinity should present a nearly linear velocity gradient or shear varying randomly in time (Lazier and Mann 1989; Jiménez, 1997; Gargett, 1997). The shear environment for a particular cell depends not only upon its size, but also on ε (the energy dissipation rate). At small scales, intermittence is a general feature of turbulent flows and is related to the presence of strong coherent vortices, with diameters of the order of ten times the Kolmogorov scale, but much longer lengths. These events should be very intense from the point of view of plankton, but calculations show that their probability is small (Jiménez, 1997). In terms of classical fluid dynamic parameters, the relevant characteristics of the velocity field, concerning direct effects on algae, can be described by ε, by the rate of strain parameter γ (T^{-1}) and by the shear stress, $\tau \approx \mu du/dz$, (MLT^{-2}), where $\mu = \rho\nu$ is the dynamic viscosity (Thomas and Gibson 1990a, b). The rate of strain parameter is proportional to a velocity gradient or shear and represents the magnitude of the deformation rate due to mean velocity gradients in the flow field; it is dimensionally equivalent to $(\varepsilon/\nu)^{1/2}$ A formal treatment of this subject can be found in Tennekes and Lumley (1972).

Effects on nutrient uptake

Solid surfaces submerged in water generate around them a layer of reduced fluid movement or boundary layer, due to the stress or drag exerted by the solid. In the outer part of the boundary layer, the stress is transmitted by eddy diffusion, but in the layers closer to the solid, turbulence is smoothed out by viscosity, and transport of substances is basically controlled by molecular diffusion. In a classical paper, Munk and Riley (1952) studied the limitations imposed by molecular diffusion on the potential rates of nutrient uptake (or metabolite excretion) by phytoplankton cells and derived expressions to calculate nutrient uptake rates by cells of different sizes and shapes. Munk and Riley (1952) also examined the effects of cell motion relative to the water (either by swimming, sinking or turbulence) on reducing the limitations imposed by molecular diffusion. They concluded that the effects of turbulence were negligible. The consideration of Michaelis-Menten kinetics together with diffusion was introduced by Pasciak and Gavis (1974, 1975) who showed that diffusion transport could be a severe limitation for cell metabolism when nutrient concentrations were low. Later, the arguments of Munk and Riley were recast by Gavis (1976) in terms of the interaction between diffusion transport and biological control of nutrient uptake rates. He concluded that nutrient transport limitation could alter competitive relationships and that motion could reduce transport limitation but not eliminate it completely. The subject was examined again by Lazier and Mann (1989), who published a comparison of the results of several authors regarding the effects of sinking and swimming and used the experimental results of Purcell (1978) to evaluate the effects of turbulence. The main conclusion (Mann and Lazier, 1991) was that sinking or swimming would have significant effects only for cell sizes exceeding a few tens of micrometres and that the effects of strong turbulence would be small compared to those of relative motion but would be appreciable for stationary cells greater than 100 μm in diameter. Recently, Karp-Boss *et al*. (1996) revised previous solutions for nutrient transfer to planktonic autotrophs and osmotrophs and extended some of these solutions to new parameter domains and flow environments including stagnant water, uniform flows (cells swimming or sinking in stagnant water), steady shear flows and fluctuating shear arising from dissipation of turbulence. The relationship between nutrient flux and cell size was found to change depending on the mechanism inducing the relative motion. The analysis of Karp-Boss *et al*., suggested that flow effects from swimming and sinking were smaller than previously accepted. For instance, a cell radius near 20 μm was needed to obtain a 50% increase of nutrient influx in comparison with that in stationary cells. On the other hand, these authors found that the effects of turbulence were an order of magnitude greater than generally supposed and represented a substantial gain for cell sizes larger than 60 μm. Interestingly, they noted that strong turbulence can reduce nutrient flux for motile organisms if it hinders them from maintaining a swimming direction parallel to the direction of shear (Fig. 4).

Notwithstanding, quantitative differences in size relationships, all theories agree with the common observation that flagellates dominate in calm oligotrophic water, where relative motion and the ability to reach areas of higher nutrient concentration may lead to enhanced survival rates. It is a common observation that some level of agitation may increase growth rates of many phytoplankton species in culture. However, few experiments have been designed to test theoretical predictions and most of that have were conducted under unrealistic (with respect to the natural environment) or unquantified physical conditions (Peters and Marrasé, pers. comm.). Pasciak and Gavis (1975) found that shear flow induced an increase in the uptake of nitrate by the diatom *Ditylum brightwellii*. Canelli and Fuhs (1976) studied the effect of sinking rates on nutrient uptake by diatoms, but their work has been criticized (Karp-Boss *et al*., 1996) on the grounds that the experimental setup was not adequate. Savidge (1981) found that agitation of the culture increased nitrate uptake of the diatom *Phaeodactylum tricornutum* but decreased its phosphate uptake, thus indicating that the effects of turbulence on nutrient uptake were complex.

The repercussions of the diverse morphological features of phytoplankton on nutrient uptake are difficult to interpret and there is an important need for experimental data on the interactions between cell properties and turbulence on nutrient uptake. As suggested by Margalef (1978, 1997) and Karp-Boss *et al*. (1996), among others, colony formation or the presence of appendages such as horns or spines could represent mechanisms to change the effective size in order to enhance relative motion or otherwise take advantage of turbulent flow fields. In a differ-

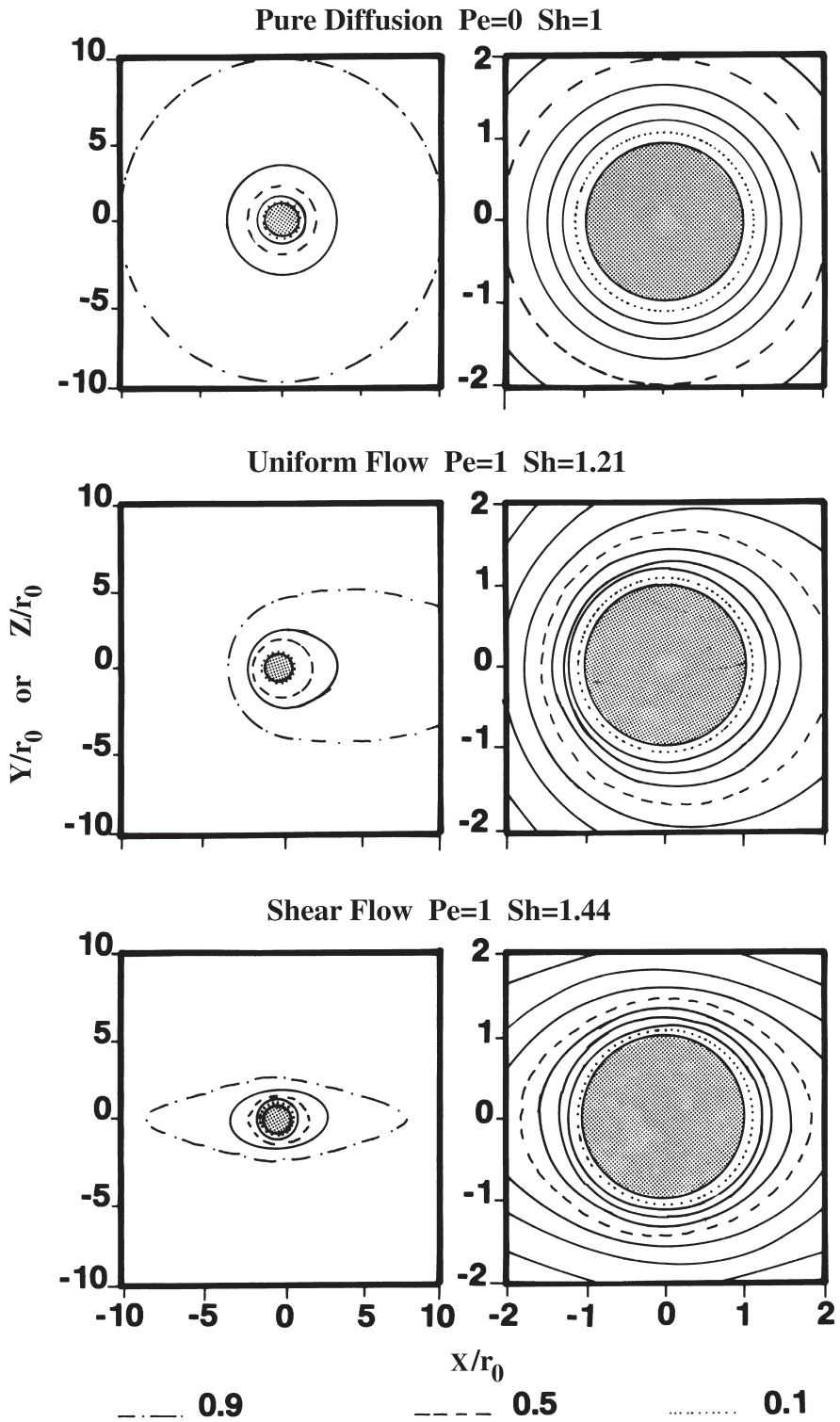

FIG. 4. – Scheme of the concentration distributions of a nutrient around a cell in three different flow regimes. Above: stagnant water. Centre: uniform flow (cells swimming and sinking in stagnant water). Bottom: shear flow. The cell is moving from right to left so that the flow is from left to right. Left panels: concentration field at distances up to 10 cell radii from the centre of the cell. Right panels: id for a distance of 2 radii. The ordinates indicate spatial dimensions (*X*, *Y* or *Z*) normalized by the cell radius, r_0. *Pe* is the Péclet number, which expresses the effectiveness of advective versus diffusive transport through the fluid over a particular length scale. *Sh* is the Sherwood number, which is the ratio between the flux of nutrients to the cell surface in the presence of fluid motion and the flux caused only by diffusion. Redrawn with permission of the authors (Karp-Boss *et al*. 1996).

ent context, the production of mucilage could play a role in controlling diffusion coefficients (Jenkinson, 1986; Margalef, 1997). A thorough review of the existing information on the relationships between turbulence, cell size and nutrient uptake can be found in Kiørboe (1993).

Microzones

The presence of relatively high nutrient concentrations in boundary layers around excreting organisms has been suggested as one possible explanation for the maintenance of relatively high phytoplankton growth rates in oligotrophic areas with very low background nutrient concentrations (McCarthy and Goldman, 1979). Experimental support for this hypothesis was provided by Lehman and Scavia (1982a, b) who observed, using autoradiography, that the chlorophyte *Chlamydomonas* took labelled phosphorus excreted by the crustacean *Daphnia*. In contrast, Jackson (1980) indicated that the nutrient excreted by the zooplankton would diffuse too fast to be used by the phytoplankton. Similarly, Currie (1984) presented his view that a microscale patch nutrient supply regime would not result in an elevated phytoplankton growth rate. A critical summary of the whole controversy (Mann and Lazier, 1991) agreed that micronutrient patches may have small significance on phytoplankton growth.

The issue of boundary layer formation and maintenance is also relevant to the potential role of microscopic and macroscopic organic aggregates (marine snow) in providing sites of attachment for autotrophs, micro-grazers and bacteria, and patches of enhanced nutrient recycling due to microbial food web activity (Silver *et al*., 1978; Mitchell *et al*., 1985). The effects of cell size on the formation of pH microenvironments were demonstrated by Richardson and Stolzenbach (1995), who showed that extracellular oxidation of Mn could be detected around phytoplankton larger than 20 μm. Evidence of pH and oxygen concentration gradients around macroscopic particles was obtained by Alldredge and Cohen (1987) using microelectrodes. The authors concluded that high nutrient concentrations in boundary layers around marine snow could play an important role in nutrient recycling.

It has been suggested that the low rate of nitrogen fixation in marine waters could be related to low concentrations of organic matter and high turbulence levels relative to fresh water environments. Turbulence of enough intensity could disrupt *Trichodesmium* colonies (Carpenter and Price, 1976) or reduce the likelihood of oxygen-depleted microzones around cyanobacterial cells (Paerl and Bebout, 1988; Paerl *et al*., 1995). However, this last hypothesis has been criticized by Howarth *et al*. (1993) and Howarth *et al*. (1995). As happens with other possible small-scale effects of turbulence, there is little conclusive experimental information concerning the relevance of microzones for marine phytoplankton life.

Effects of small-scale turbulence on phytoplankton growth and cell division

Agitation of cells of phytoplankton or other kinds of organisms in cultures, whether by bubbling, oscillating grids, rotating paddles or other mechanisms is often used as a means of enhancing growth rate (Aguilera *et al*., 1994). As described above, the explanation for this effect presumably lies in the influence of relative motion in breaking boundary layers and increasing chemical gradients around the cells. Of course, sufficiently high levels of turbulence may be expected to cause cell damage. Different algal groups have shown susceptibility to moderate levels of agitation (e.g. Fogg and Than-Tun, 1960; Schöne, 1970), but dinoflagellates appear to be specially sensitive (White, 1976).

A number of publications have described effects of agitation on non-dinoflagellates, but without an evaluation of the intensity of turbulence in fluid dynamical terms. For instance, the growth of the cyanobacterium *Anabaena cylindrica* increased up to a shaking rate of 90 oscillations per minute, but decreased at higher shaking rates (Fogg and Than-Tun, 1960). In contrast, Volk and Phinney (1968) described inhibitory effects of agitation for *Anabaena spiroides*. In the case of the diatom *Phaeodactylum tricornutum*, Savidge (1981) reported that cell division times in the exponential phase decreased with increasing agitation of phosphate-limited cultures, but increased in nitrate-limited cultures. Schöne (1970) showed that the intensity of the motion of the sea surface (in a categorical scale) was inversely related to chain length of several colony-forming diatoms like *Chaetoceros curvisetus* and *Skeletonema costatum*. The diminution of chain length with increasing motion was apparently due to mechanical breaking-up of chains. He could produce similar effects using air bubbling of *S. costatum* cultures in the laboratory. Other effects of agitation were more subtle, such as the synchronization of cell divi-

sion in *S. costatum* populations, after only 5 min of agitation per day. Bakus (1973) carried out competition experiments between *Scenedesmus* (chlorophyte) and *Stichococcus* (generally classified as chlorophyte), under varying conditions of irradiance and aeration. He found that the advantage in the final yield of *Scenedesmus* over *Stichococcus* could be reversed in the presence of a combination of turbulent water movements and decreased illumination.

The effect of turbulence on dinoflagellates appears to be generally negative. Mention of inhibitory effects of aeration on dinoflagellates was made by Tuttle and Loeblich (1975) and Galleron (1976). Deleterious effects of water motion on dinoflagellates include disturbance of cell division, morphological changes, cell disruption and interference with organism behaviour. These observations, which present a practical interest due to the implication of dinoflagellates in many harmful algal events (with or without blooms) have been recently reviewed by Estrada and Berdalet (in press). White (1976) reported that death and disintegration of *Alexandrium fundyense* (= *Gonyaulax excavata*) occurred in cultures under continuous rotary shaking at speeds of 125 rpm and greater; intermittent shaking during periods of only 30 min d^{-1} caused growth inhibition. In Lake Kinneret, the division rate of *Peridinium gatunense* (= *Peridinium cinctum* forma *westii*) was inhibited during wind episodes (speed exceeding 3.5 m s^{-1}) that occurred between 18:00 and 02:00 h (Pollingher and Zemel, 1981). This time period corresponded to the premitotic and mitotic phases of cell division. In contrast, even intense winds blowing during the day did not affect the division rate of the dinoflagellate. The relationship between water turbulence and division rate of *P. gatunense* was tested experimentally using rotary shaking at 100 rpm in the laboratory. Cell mortality and decreased division rates with respect to the controls were caused by continuous shaking. Intermittent shaking (2 h d^{-1}) inhibited cell division during the dark, but not during the day. Berdalet (1992) showed that cell division of *Gymnodinium nelsonii* was prevented and cell volumes increased when cultures were placed in an orbital shaker at 100 rpm. In addition, the cellular concentrations of RNA and DNA increased up to 10 times those of the controls (Fig. 5). Berdalet and Estrada (1993) and Estrada and Berdalet (in press) reported similar results with *Alexandrium minutum*, *Prorocentrum micans* and *Prorocentrum triestinum*, but found that a small *Gymnodinium* sp. (10 μm in diameter) was not affected by shaking at 100 rpm. From a survey of their experimental data, Estrada and Berdalet (in press) concluded that, for comparable levels of water motion or energy input, deleterious effects appeared to be stronger for larger organisms and for smaller culture vessels. This could be expected from

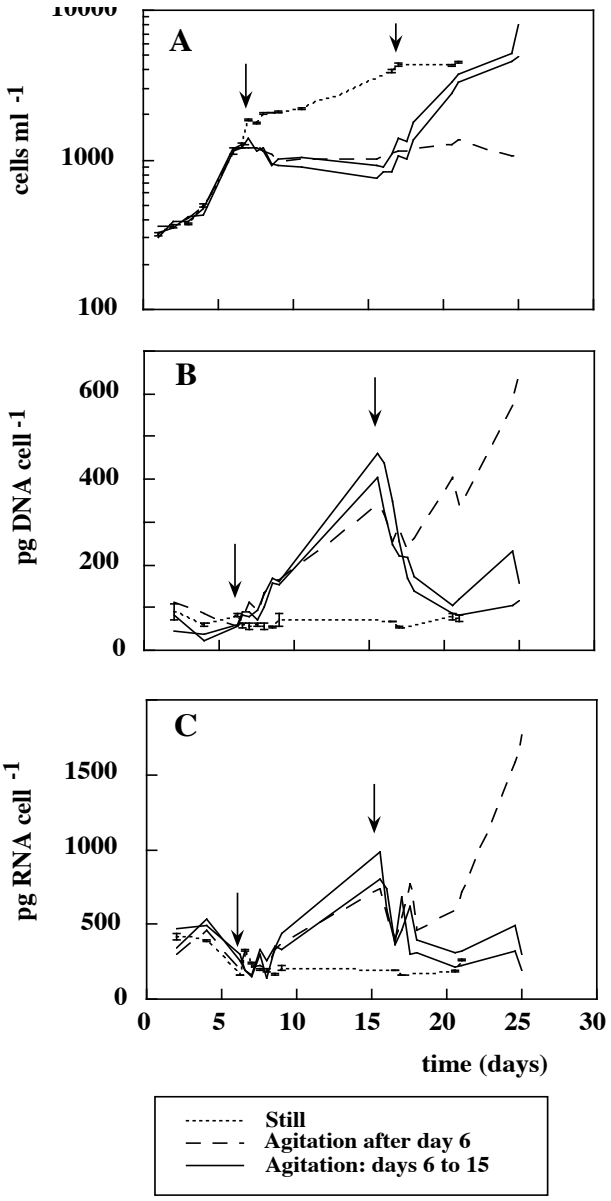

FIG. 5. – Effect of agitation on the dinoflagellate *Gymnodinium nelsonii* in terms of cell numbers (A) and concentrations of DNA (B) and RNA (C) per cell. Three flasks were kept under still conditions (dotted lines, average ± SE). Two flasks (continuous lines) were placed in an orbital shaker (at 100 rpm) from day 6th to 15th (indicated by the two arrows). One flask (dashed line) was agitated since day 6th until the end of the experiment. Cessation of culture development occurred since the beginning of agitation (A), concomitant with the increase in nucleic acids per cell (B and C). Cell recovery and return to the usual DNA and RNA content occurred when the cultures were returned to still conditions. Redrawn with permission from Berdalet (1992).

fluid dynamic considerations, because the energy imparted by the orbital shaker is similar for a large than for a small vessel, but it is dissipated into a larger volume of fluid in a larger vessel. Regarding size, for the same turbulence intensity, velocity differences across a large cell will be larger than across a small cell.

The increase in nucleic acid content of dinoflagellate cells exposed to inhibitory turbulence levels (Fig. 5) suggests that effects on cell division may be related to impairment of chromosome separation after DNA duplication (Berdalet, 1992). Other cellular processes, such as nutrient uptake or photosynthetic activity appear to be less sensitive to turbulence (Berdalet, 1992; Thomas *et al.*, 1995). Dinoflagellates possess a cytoplasmic spindle and it has been speculated that blockage of cell division by agitation could be due to physical disturbance of the microtubule assemblage (Karentz, 1987; Berdalet 1992). However, no microscopical evidence is available yet.

Experimental studies comparing the effects of different levels of turbulence on phytoplankton are scarce and only in few cases the intensity of turbulence is expressed in terms of fluid dynamic parameters (Dempsey, 1982; Thomas and Gibson, 1990a, b). An additional complication is that the culture devices used to facilitate the calculation of physical parameters may not provide adequate culture conditions (Peters and Redondo, 1997). This was the case with the paddle stirrers used by Dempsey (1982). Thomas and Gibson (1990a, b) used Couette devices to study the effects of known shear rates on *Lingulodinium polyedrum* (= *Gonyaulax polyedra*). They found that the turbulent dissipation rate threshold for growth inhibition was about 0.18 $cm^2\ s^{-3}$. However, the fact that in these Couette instruments the organisms were kept between two concentric cylinders, in a space of only 0.5 cm, could cause some problems.

A summary of estimates of Kolmogorov length scales and strain rates for natural environments and experimental systems including animal and algal cell cultures is given in Table 1, together with calculated values of the average turbulent energy dissipation generated by wind in the upper 10 m. A survey of the available data (Peters and Marrasé, pers. comm.) showed that negative effects of turbulence on phytoplankton growth seemed to appear at turbulent kinetic energy dissipation rates (ε) exceeding 0.1 $cm^2\ s^{-3}$, in basic agreement with the conclusions of Thomas and Gibson (1990b). As can be seen in Table 1, an ε of 0.1 $cm^2\ s^{-3}$ corresponds to turbulence levels above those found typically in marine waters, although higher ε values have been recorded in estuaries or tidal fronts. Turbulence levels with ε

TABLE 1. – A: Rates of turbulent energy dissipation (ε), Kolmogorov length scales (λ_v)and strain rates (γ) for natural systems. B: id. for experimental systems. C: Average turbulent energy dissipation generated by wind in the upper 10 m (ε) and corresponding λ_v and γ (taken from Kiørboe and Saiz, 1995, calculated according to Mackenzie and Legget, 1993). References: 1, Reynolds (1994); 2, Kiørboe and Saiz (1995), with data compiled by Granata and Dickey, 1991; 3, Lakhotia and Papoutsakis (1992); 4, Thomas and Gibson (1990b); 5, Dempsey (1982).

A. Natural systems	ε ($cm^2\ s^{-3}$)	λ_v (mm)	γ (s^{-1})	Ref
Lakes	$0.014\ 10^{-2}$-$4\ 10^{-2}$	0.7-2.9	0.1-2.1	1
Open ocean	10^{-6} -10^{-2}	1-0.10	0.01-1.	2
Shelf	10^{-3} -10^{-2}	0.18-0.10	0.32-1.	2
Coastal zone	10^{-3}-10^{0}	0.18-0.03	1.0-10.	2
Tidal front	10^{-1}	0.06	3.16	2
Tidal estuary (Severn)	$2.2\text{-}8\ 10^{-2}$	$1.3\ 10^{-1}$-$4.3\ 10^{2}$	0.2-0.67	1
B. Experimental systems				
Animal cell cultures	0.6-1.	0.36-0.31	7.7-11	3
Couette cylinders				
Range	0.045-164	0.08-0.66	2.2-132	
Effect threshold	0.18	0.48	4.4	4
Paddle stirrer	0.096-0.14	0.62-0.52	3.1-3.7	5
C. Model				
Wind speed ($m\ s^{-1}$)				
5	$1.7\ 10^{-3}$	0.16	0.4	—
10	$1.5\ 10^{-2}$	0.09	1.2	—
15	$4.9\ 10^{-2}$	0.07	2.2	—
20	$8.4\ 10^{-2}$	0.06	2.9	—

exceeding 10^2 cm^2 s^{-3} can be found in surf zones (George *et al*., 1994). According to Gibson and Thomas (1995), the action of intermittent wave breaking could be sufficient to cause cellular effects on dinoflagellates. These observations lead us to speculate that direct effects of turbulence on phytoplankton cells could be important, for example, in shallow estuarine areas subjected to intense winds.

In addition to disturbances of division or mechanical cell damage, several studies have suggested the possibility of more subtle effects, probably due to the interference of intense turbulence with swimming, migration or other behavioural features of the dinoflagellates (White, 1976). This kind of mechanism was advocated by Estrada *et al*. (1987a) as a possible explanation of the results of a microcosms experiment in which they applied different agitation treatments to 30 l culture vessels. They found that a diverse dinoflagellate community thrived in containers agitated by oscillating grids at 20 rpm, while all dinoflagellates died out in vessels with stagnant water or subjected to higher turbulence levels. In another microcosm experiment, Estrada *et al*. (1987b) observed that dinoflagellates did not grow in cylindric containers that were illuminated only in their lower part. The authors speculated that this unusual irradiance gradient could interfere with the migration behaviour of dinoflagellates.

Other cellular effects. Bioluminiscence

Many dinoflagellates present bioluminescent activity when stimulated. Anderson *et al*. (1988) measured the luminescent response of *Gonyaulax* using laminar flow in a capillary tube and found that bioluminiscence appeared at the entrance to the tube, after a change in diameter presumably inducing turbulent water motion. The effect of laminar shear associated with Couette flow on several dinoflagellate species and plankton assemblages was studied by Latz *et al*. (1994), who showed that the excitation threshold for bioluminiscence was several orders of magnitude greater than typical oceanic shear stress values in the mixed layers, with the possible exception of surface-breaking waves. Rohr *et al*. (1990) examined the bioluminescence of sea water samples containing dinoflagellates over a wide range of laminar and turbulent pipe flows. They observed a dramatic increase in the bioluminescent activity at the transition from laminar to turbulent flow, which occurred at Reynolds numbers between 4000 and 8000 and strain rates between 2350 and 1915 s^{-1}, again much higher than typical values in the ocean. Bioluminiscence increased with increasing turbulence. This was due to the stimulation of more organisms rather than an increase in individual light levels. The Kolmogorov length scale in the pipe flow at Re=4000 was estimated to be 33 μm, similar or slightly smaller than the bioluminescent plankton present in the samples.

CONCLUDING REMARKS

Water turbulence is a fundamental factor in phytoplankton ecology. The variety of physiological and morphological properties of phytoplankton may be largely considered as adaptations to different scales and characteristics of turbulent motions in the aquatic environment. The conceptual model of Margalef (1978), which proposes an ordination of phytoplankton life-forms in relationship with their adaptation to turbulence intensity and nutrient availability as dominant environmental factors, has provided a useful framework for understanding the basic strategies of phytoplanktonic life. However, there are large gaps in our knowledge of the interactions between turbulent flow fields and phytoplankton organisms, as could be expected from an area of knowledge which combines the difficulties of studying turbulence with those of understanding phytoplankton biology. At the large and mesoscale levels, there are questions concerning coupling between hydrographic features and quantitative and qualitative changes in the phytoplankton community. This subject is basic to improve our understanding of the selection and accumulation of particular assemblages and life forms and could have practical implications concerning food web relationships and harmful algal phenomena. It would be very important to develop new biological sampling methodologies allowing for spatio-temporal resolutions comparable to those used in physics. Fluorescence-based sensors, flow cytometry and remote sensing techniques are steps in this direction. Regarding the small scales, future experimental research should consider the use of realistic turbulence conditions. The main lines of investigation should cover the implications of cell size and shape on nutrient incorporation and light utilization in a turbulent environment, the relevance of microzones, the influence of turbulence on food web interactions and the possible direct effects of turbulence on phytoplankton organisms. Interdisciplinary research on the interaction

between turbulence and phytoplankton life represents a promising challenge which could take advantage of the availability of new computing and instrumentation developments.

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